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## SUPERNUMERARY CHROMOSOMES, AND SYNAPSIS IN CEUTHOPHILUS (SP.?).

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The species of *Ceuthophilus* which I have used in this study, I have not been able to identify. The material seems to be homogeneous, and is the only species of this genus that I have seen about Bryn Mawr. The insects were found, usually in pairs, in their burrows under stones, and were collected in October and November, 1910 and 1911. They are not abundant, and only 7 males were secured in 1910, and 5 in 1911.

### METHODS.

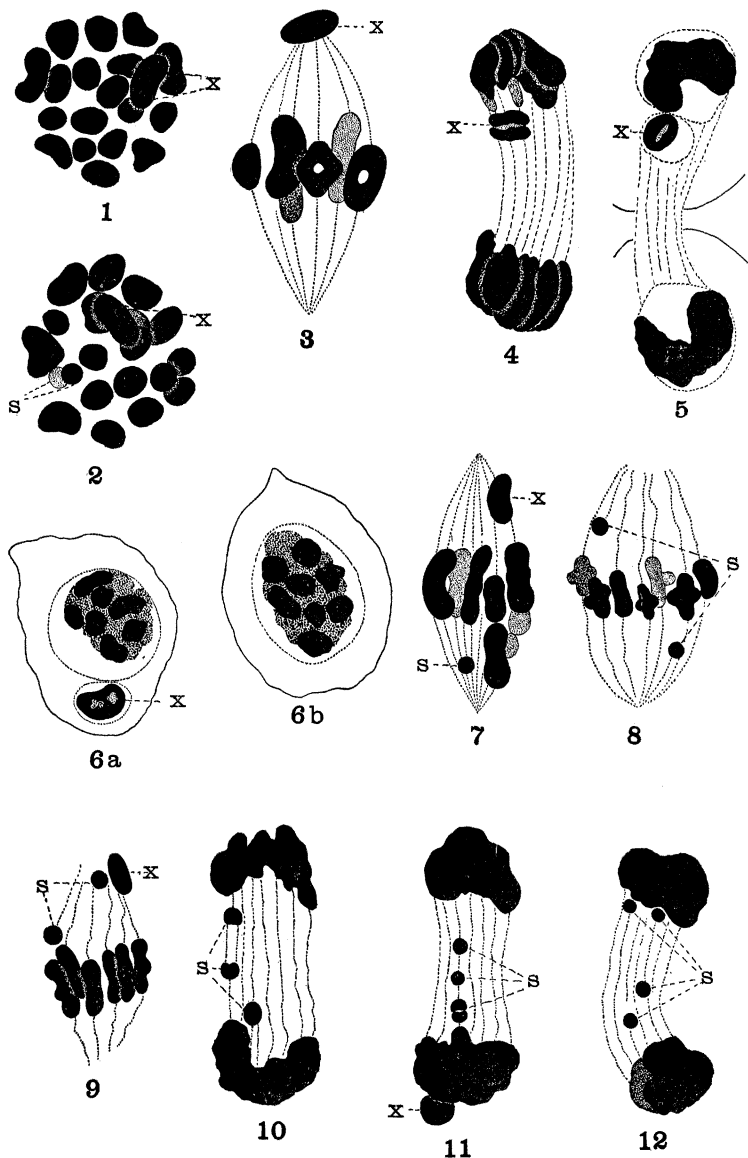
In the case of each individual a few aceto-carmin preparations were made, and the remainder of the testes fixed in Gilson's mercurio-nitric fluid or in Flemming's stronger chrom-osmic-acetic mixture. The best results were obtained from sections of Flemming material, cut  $10\mu$  thick and stained with thionin.

### SUPERNUMERARY CHROMOSOMES.

In one of the 1910 insects one, and in another two supernumerary chromosomes were found. These chromosomes are readily distinguished from the other chromosomes by their smaller size and erratic behavior.

The spermatogonial chromosomes, like those of *Stenopelmatus*, are difficult to count, because they do not form a flat plate at any stage, but lie at somewhat different levels and overlap. The number is probably 37, exclusive of supernumeraries.

In the first spermatocytes there are 18 bivalents and the univalent *X* (19), when no supernumeraries are present (Fig. 1). Fig. 2 shows 18 bivalents, the unpaired chromosome *X*, and 2 supernumeraries (*s*). The odd chromosome *X* is usually found at one pole of the spindle when the other chromosomes are in metaphase (Fig. 3), but it not infrequently lags behind the others in the anaphase (Fig. 4) and is enclosed in a separate membrane



FIGS. 1-2. Metaphase of first maturation mitosis, showing  $18+X$  and  $18+X+2s$ . (Mag. 1,500 for all figures.)

FIGS. 3-5. Metaphase and anaphases showing position of  $X$ .

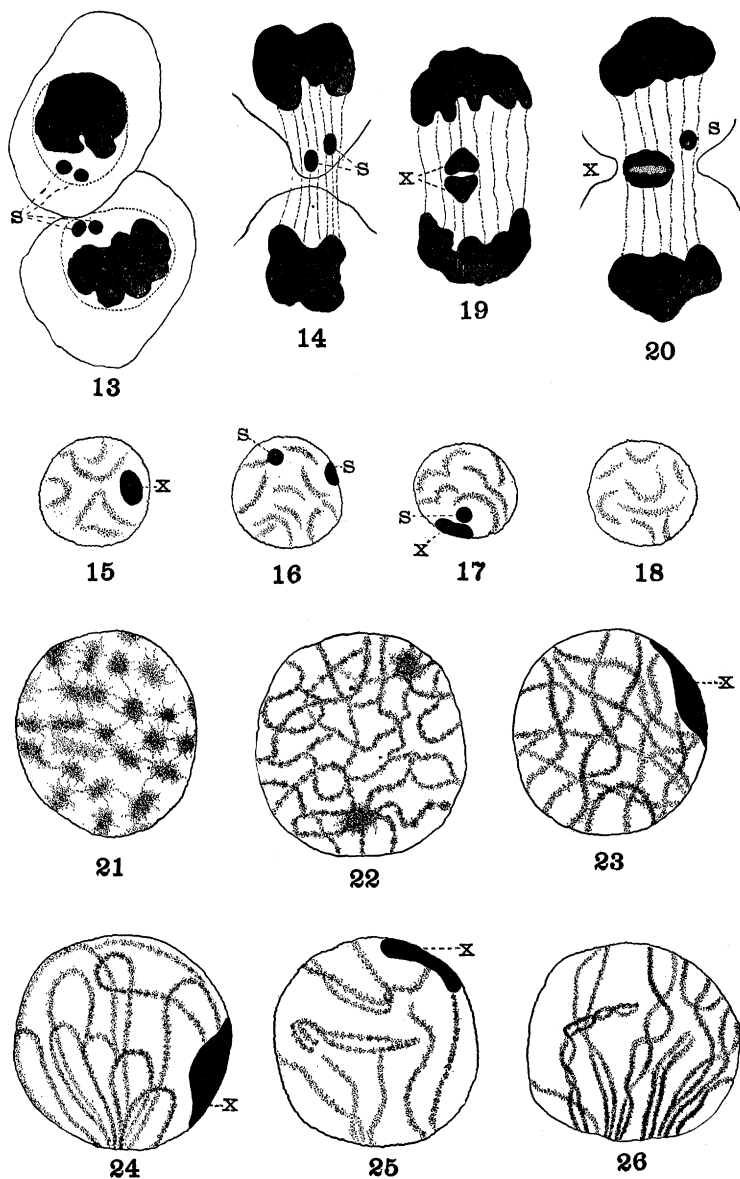
FIGS. 6a and b. Young sister spermatocytes of the second order.

FIGS. 7-12. Variations in position and division of the two supernumeraries in first spermatocytes.

in the telophase (Fig. 5). Figs. 6a and 6b are sister spermatocytes of the second order, showing  $X$  in a separate vesicle; this does not happen in by any means one half of the second spermatocytes,  $X$  being, I should say, more often included within the same nuclear membrane with the other chromosomes.

Fig. 7 is from the individual which had one supernumerary, and Figs. 8 to 14 from the one that had two. Fig. 8 also shows a less usual position of  $X$ , near the equatorial plate. As in the *Diabrotica* (Stevens, '08) the supernumeraries may or may not divide in the first maturation mitosis, and they may, when undivided, go to either pole of the spindle. Their position in the metaphase does not necessarily indicate whether they will divide or not. The determining factor is probably the attachment of spindle fibers from one or from both poles. The supernumeraries in Figs. 7, 8 and 9 would not divide in this mitosis, but the presence of a supernumerary in an equatorial plate or between daughter plates does not necessarily assure its division. In Fig. 10 one is divided, the other undivided, while in Figs. 11 and 12 both are divided. In the telophases shown in Figs. 13 and 14, both supernumeraries are divided in one case and neither in the other. The possible combinations of  $X$  and the 2 supernumeraries in the spermatids are  $X$ ,  $X + 1s$ ,  $X + 2s$ , 0,  $1s$  and  $2s$ . Four of the possibilities are shown in Figs. 15 to 18.

As to the origin of these supernumeraries, there is little evidence in this material. In *Metapodius* Wilson ('09) discovered the probable origin of the supernumeraries in an irregular second spermatocyte mitosis in which both "idiochromosomes" went to the same pole of the spindle, and therefore to the same spermatid. The supernumeraries are thus shown to be duplicates of the smaller "idiochromosome" in *Metapodius*, or in one case of an "*m*-chromosome" ('10). In neither *Diabrotica* nor in *Ceuthophilus* is there a smaller mate for the  $X$  chromosome present. The three supernumeraries which have been observed in *Ceuthophilus* are of about the same size; considerably less than one half, and apparently about one fourth the size of  $X$ . The behavior of the supernumeraries in growth and rest stages of the nucleus indicates their probable relationship to  $X$ , and their behavior in mitosis, dividing only once, either in the first or the second



FIGS. 13-14. Telophases showing the supernumeraries divided (13) or undivided (14).

FIGS. 15-18. Spermatized nuclei showing variations as to presence or absence of X and the two supernumeraries.

FIGS. 19-20. Anaphases showing unusual position of X.

maturation mitosis, shows that they are univalent. In *Diabrotica soror* I have considerable evidence that the supernumeraries owe their origin to a transverse and a longitudinal division of  $X$  ('12), and it seems probable that those of *Ceuthophilus* have had a similar origin. I have occasionally found cases where  $X$  seemed about to divide late in the first maturation mitosis (Figs. 19 and 20), but I have as yet no evidence of a transverse division.

#### SYNOPSIS.

The material which was collected in 1911 with the hope of getting more light on the origin of the supernumeraries, proved to be favorable for a study of synapsis, or, as I should prefer to call the phenomenon, conjugation of the chromosomes. These testes were all fixed in Flemming and stained with either thionin or iron-hæmatoxylin. Thionin gave the clearest figures.

In the resting nuclei of the spermatogonia the chromosomes are either visible as separate individuals as in Fig. 21, or are more or less completely resolved into rather fine spireme threads as in Fig. 22. In some follicles one sees only such spermatogonial nuclei as in Fig. 21; in others the various cysts show various degrees of resolution into spireme threads. The former condition I should attribute to more rapid division of the spermatogonia, the time between mitoses being insufficient for complete resolution.

In the youngest spermatocytes, distinguished from the spermatogonia by the condensed condition of  $X$ , the spireme threads are similar to those of the spermatogonia, perhaps a little coarser. They are finely granular and more or less nodular. There is no contraction, or synizesis, stage and no complete polarization of loops to form a perfect bouquet stage. The spireme threads are usually irregularly but rather evenly distributed through the nucleus as in Fig. 23, which also shows  $X$  in characteristic position against the nuclear membrane. Fig. 24 shows an extreme and

FIGS. 21-22. Spermatogonial nuclei, showing resolved and unresolved chromosomes.

FIG. 23. Spermatocyte nucleus before synapsis.

FIG. 24. Similar stage showing partial polarization of chromosomes.

FIGS. 25-26. Stages in parasynapsis.

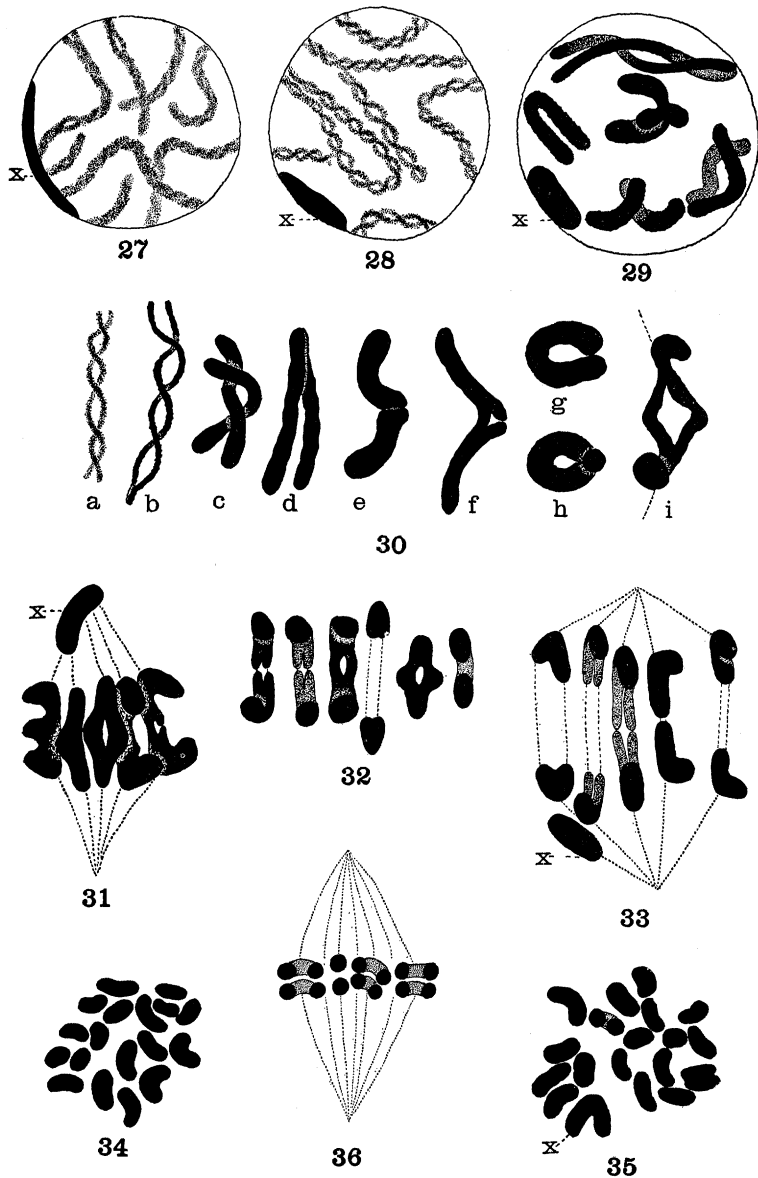


FIG. 27. Double spireme stage.

FIGS. 28-29. Prophase stages.

FIG. 30*a-i*. Various prophase (*a-g*) and metaphase (*h, i*) forms of the bivalent chromosomes.

FIGS. 31-32. Chromosomes in metaphase of the first maturation mitosis.

unusual case of polarization, but here only nine polarized loops are present and the other spireme threads extended in various directions through the nucleus. In some follicles there is a perfectly sharp division-line between cysts containing spermatocyte nuclei of the character of that shown in Fig. 23, and cysts in which the spireme is about twice as thick (Fig. 27). There is no evidence of telosynapsis, and also no evidence of any such longitudinal contraction of the threads as would be required to give the thicker spireme of Fig. 27. In other follicles there come in between these two stages, other cysts in which as a rule the chromatin threads are very irregularly distributed; *i. e.*, there is a conspicuous absence of the rather even spacing of the threads observed in Figs. 22 and 23. Careful inspection of such cysts reveals various stages in pairing, conjugations, or synapsis of the chromatin threads (Figs. 25 and 26). In the same cyst one often finds various stages,—only one or two pairs and the other threads single as in Fig. 25, and all stages up to one in which all of the threads are in pairs. Occasionally some of the pairs in a nucleus show as much polarization as is indicated in Fig. 26, but in the same nucleus other pairs are differently distributed. There is never such complete polarization as is shown in some of the figures of Grégoire ('10), the Schreiners ('04), Agar ('11) and others. The occurrence of various stages of parasynapsis in the same cyst, the substantial agreement in size of the chromatin threads through the stages indicated in Figs. 23–26, and the spireme of double size in the next stage, preclude the possibility of interpreting the paired condition seen in Figs. 25 and 26 as a longitudinal split. Homologous chromosomes in some way come together, and gradually twist up into a tighter and tighter rope-like strand. A casual comparison of cysts in the stage shown in Fig. 27 with the earlier stages (Figs. 23 to 26), using low powers of the microscope, simply gives the impression that here we have a spireme, or sections of a spireme, twice as thick as in the previous stages, but study of such nuclei with Zeiss 1.5 mm. and oc. 12 reveals the double and twisted condition of the strands

FIG. 33. Anaphase showing segregation of homologous chromosomes and longitudinal splitting.

FIGS. 34–36. Second maturation mitosis showing dimorphism in number (18 and 19) and equational division.



in practically every nucleus, indicating that the paired threads are at no time so thoroughly fused as even apparently to lose their identity. This is further indicated by the earliest prophase stage (Fig. 28) where the paired strands begin to untwist. The following prophase stages consist of further untwisting and longitudinal contraction of the paired homologous chromosomes. In the synapsis stage (Figs. 25 and 26) it is impossible to tell whether threads of equal length form the pairs, but in the prophase pairs this is perfectly evident (Figs. 29 and 30). The untwisting and contraction frequently proceed at different rates in different pairs in the same nucleus and in different nuclei of the same cyst, so that one can easily compare the various stages of the process and be perfectly sure that the untwisting is continuous. There is no secondary fusion of paired threads such as frequently occurs in cases where a precocious longitudinal split appears in a telosynaptic bivalent and then closes up before the rings and crosses are formed (see *Blattilla germanica*, Stevens, '05). Fig. 30 shows various stages in the formation of the definitive chromosomes of the first maturation mitosis from the parasynaptic threads of a stage a little later than that of Fig. 28. The paired chromosomes untwist and contract simultaneously. Some remain united at one end (*b* and *d*) while in other cases union of a pair at one or both ends is a secondary phenomenon and may even occur after the spindle has formed (*a* and *c*). That there is much variation in the form and size of the 18 bivalents in metaphase is shown in Figs. 3, 7, 8, 9, 30, 31, 32 and 33. The most frequent forms are rings, E's and crosses, though one or more pairs of straight rods may be found in nearly every spindle. Most of the chromosomes are attached to the spindle fibers at or near the middle of each univalent member of the pair, so that the separated chromosomes pass to the poles of the spindle in the form of V's (Figs. 31 to 33). In the case of the double rods the fibers are attached at the ends. Many of the chromosomes are partly or wholly split longitudinally in the anaphase (Fig. 33). There are of course two kinds of second spermatocyte equatorial plates containing 18 and 19 chromosomes respectively (Figs. 34 and 35), X appearing in the form of a large V (Fig. 35) in one half of the cells. Division of the chromosomes is here longitudinal as seen in Fig. 36.

In *Ceuthophilus* the first maturation mitosis is therefore a segregating division of the previously paired and united homologous univalent chromosomes, while the second mitosis is as clearly an equational division of all of the univalent chromosomes including *X*.

#### DISCUSSION.

In an earlier study ('05) of the spermatogenesis of two other species of Orthoptera, *Blattella (Blatta) germanica* and *Stenopelmatus* (sp.?), I found what seemed to be good evidence of telosynapsis ('05, Pl. II., Figs. 55, 56, 58, 59, 62, 63, 64, and Pl. III., Figs. 108 to 115). That material I have reviewed and compared with the *Ceuthophilus* preparations, and I find no such evidence of parasynapsis in either of them. Naturally I expected to find telosynapsis in *Ceuthophilus*, and was surprised on working backward from the maturation mitoses to find no evidence of telosynapsis outside of the late prophases, and abundant evidence of parasynapsis in the young spermatocytes at a stage where synizesis is frequently found in other material.

A recent review of the literature on conjugation of chromosomes has only strengthened my previous conviction, based on my own experience with the spermatogenesis of a variety of forms, that the phenomenon is one which varies greatly in different groups of organisms, and even in different species of the same genus, or different sexes of the same species (*Sagitta*, Stevens '03, '05; *Bufo*, King '07, '08). Indeed I should not be surprised if the range of variation should prove to extend from (a) cases where there is nothing that could be called conjugation, but merely such a pairing, without contact even, as will secure segregation of homologous maternal and paternal chromosomes to different daughter cells, through (b) an intermediate condition of telosynapsis and less intimate parasynapsis, to (c) cases where homologous chromosomes are so completely fused in parasynapsis that it is impossible to tell whether the resulting chromosomes which are segregated in mitosis are identical with those that went into synapsis or not; and the variation may extend to cases which may give further support to Janssens' chiasma theory ('09) or to Morgan's modification of it ('11) in which homologous chromosomes are supposed to be twisted tightly together in

parasynapsis and split across the twists in preparation for mitosis, giving daughter chromosomes which contain both maternal and paternal chromatin.

In *Ceuthophilus* the parasynapsis stage of Fig. 27 is intimate enough and long enough to favor the supposition that it is a true conjugation involving exchange of material particles or of chemical substances (genes), but there is no evidence of any splitting of Morgan's chiasma type. All of the evidence indicates that homologous paternal and maternal chromosomes twist together in parasynapsis and untwist in the prophase of the first maturation mitosis. In the flies and mosquitoes (Stevens, '08, '10, '11) we have examples of even more pronounced parasynapsis than in *Ceuthophilus*, but so far as I have seen, the indications are that the chromosome pairs twist up in synapsis and untwist in prophase much as in *Ceuthophilus*; *i. e.*, an opportunity for interchange of genes between homologous maternal and paternal chromosomes is furnished by the observed phenomena of parasynapsis in these forms, but no evidence of such a chiasma type of splitting after synapsis as is suggested by Morgan ('11) to account for the results of his breeding experiments with *Drosophila*. Such an exchange of parts of chromosomes as that described by Janssens ('09) might of course occur without being detected, at almost any point in the process of twisting or untwisting of the pairs, since the time element is not determinable in fixed preparations.

Moreover, it seems to me that, in view of the great range of variation in the phenomena of conjugation and segregation of the chromosome in the maturation of germ cells, cytological evidence from one form cannot safely be taken to serve as the basis of a theory or hypothesis to account for the experimental results on another form, but cytological and experimental work on the same form must go hand in hand, in order that any safe conclusions may be drawn from the results.

There seems to be no question but that synapsis, or conjugation of the chromosomes is the most difficult phenomenon connected with the maturation of the germ cells, to interpret correctly, and doubtless earlier parasynaptic stages have been overlooked in some cases where telosynapsis alone has been described in con-

nection with the mitotic stages of maturation, but it seems to me quite unlikely that synapsis in all organisms follows one method; and, moreover, I believe that the variations in method of synapsis and intimacy of union of homologous chromosomes in different forms will be found to be directly connected with variations in methods of inheritance of unit characters, especially in relation to interchange or lack of interchange of maternal and paternal genes. If this is true we should expect to find more cases of complete coupling of unit characters where telosynapsis or no real synapsis occurs. If parasynapsis is an adaptation to secure interchange of genes, we should expect to find cases of telosynapsis followed by parasynapsis, as indicated, but not certainly demonstrated in the guinea-pig (Stevens, '11, Figs. 9, 10, 11). In my studies on spermatogenesis of the Coleoptera ('05, '06, '08, '09) I found evidence of telosynapsis in several cases and no evidence of parasynapsis, but this was only an incidental matter at the time, and of interest merely in relation to the segregation of whole chromosomes in the maturation mitoses. It is my intention to reëxamine all of my Coleoptera and Diptera material with reference to the questions whether parasynapsis occurs in the Coleoptera, and whether the Diptera show any evidence of Janssens' chiasma types of synapsis.

BRYN MAWR COLLEGE,  
January 1, 1912.

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